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AN EMBRYOLOGICAL STUDY OF LIMNOCHARIS EMARGINATA.

JOHN GALENTINE HALL.

(WITH PLATE IX)

Limnocharis emarginata is of South American origin. The plants from which material was taken for study are growing in a large tank in the aquatic house at North Easton, under conditions that appear to be normal, and are certainly favorable for propagation, as is shown by the maturing of abundant seed from the self-pollinated flowers, and the large number of seedlings that spring up spontaneously in the tank.

The discrepancies in the comparative embryology of the group to which Limnocharis belongs, as represented by the work of Marshall Ward, Schaffner, Campbell, and others, seemed to justify careful examination of the present material. I shall give no account of the general morphology, as Buchenau has described the development of the flower and of the tissue of the growing point.

The ovules in their general development follow very closely the development of the ovules of *Butomus umbellatus* as described by Marshall Ward. They arise as emergences from the walls of the carpels without definite placental arrangement. The subsequent development is of the usual angiospermous type, except the history of the embryo sac. Each integument is composed of two layers of cells, the inner being a trifle longer than the outer, and forming a considerable mass of tissue at the apex of the ovule around the micropyle, as is the case in Naias and Zannichellia. From the outer coat, soon after fertilization, certain cells begin to develop into short hairs that give the seed a rough appearance. Long before the seed coats begin to form, the growth of the ovule is more rapid on one side (*fig. 3*), and anatropy is already marked when the rudiments of the coats make their appearance (*fig. 4*).

Very early it is possible to distinguish the single hypodermal cell that forms the archesporium (*fig. 2*). It is somewhat larger than the surrounding cells, and the nucleus is considerably larger than those of the adjacent cells. There is a tapetum cut off by the archesporial cell, such as is described by Campbell for Naias and Zannichellia. In Limnocharis, however, the tapetal cell is without a wall, and it is pushed towards the apex of the sac (*fig. 4*), where it disappears in the later stages of development. The large cell left after the formation of the tapetum becomes the embryo sac without further division. About the time the first division takes place in the embryo sac the epidermal cell that overlies it divides by a periclinal wall, forming a false tapetal cell (*fig. 4*). In Butomus, according to Marshall Ward, there are two cells cut off in succession from the apex of the archesporial cells, and sometimes the first one divides once longitudinally. These three cells have very deliquescent walls, and soon disappear.

The history of the nuclear changes in the embryo sac differs considerably from the ordinary in the last stages. After the first division of the megaspore nucleus, the two daughter nuclei migrate to each end of the sac. The one that goes to the micropylar end passes through the usual divisions to form the egg apparatus and upper polar nucleus; while the one that goes to the antipodal end remains undivided (*figs. 5–8*). In Butomus, Marshall Ward says that sometimes only two nuclei are formed at the antipodal end of the sac, and that one of these fuses with the upper polar, leaving only one antipodal. The antipodal is not cut off by a wall from the sac in Limnocharis, Butomus, or Alisma, while in Sagittaria, Naias, and Zannichellia cell walls are formed around each of the antipodal nuclei.

The secondary nucleus at the micropylar end of the sac divides transversely (*fig. 5*), and then each of the resulting nuclei divides longitudinally (*figs. 6–7*), but not always simultaneously, making the usual four at that end of the sac. The lower one of the two nuclei, by division, makes the egg and upper polar; while the other forms the two synergids.

At this time, the upper polar nucleus (*fig. 8*) begins a migration toward the antipodal end of the sac, at the same time increasing somewhat in size, so that it has very much the appearance of an endosperm nucleus. This migration continues until the nucleus reaches the region of the antipodal nucleus (*fig. 9*), though no fusion takes place, for the latter can be seen in all but the very latest stages of the embryo sac and embryo. The upper polar nucleus, when it has approached the antipodal end of the sac, divides transversely (*fig. 10*). The lower daughter nucleus remains in the position of its formation, being cut off by a wall across the sac (*figs. 11–12*), and forming a large cell that does not divide further, but finally disappears through the encroachment of the endosperm. In *Butomus umbellatus*, Marshall Ward says that the two polars approach the middle of the sac, where they fuse, forming a definitive nucleus, and leaving only one antipodal nucleus. In Sagittaria, Schaffner shows a similar division of a large nucleus, and formation of a wall across the sac, near the antipodal end, which he says takes place after the fusion of the polar nuclei ; and he states that frequently the nucleus of the cell cut off toward the lower end of the sac divides to form two or three, when the embryo is in about an eight-celled stage. Campbell describes a similar large nucleus in both Naias and Zannichellia, but does not state definitely what is its origin. He makes no mention of any wall cutting it off from the rest of the endosperm, but suggests that it may be the lower polar nucleus. Such cannot possibly be the origin of the one in Limnocharis, because there is no lower polar formed. Campbell also says that the nucleus resembles the suspensor nucleus in Naias and Zannichellia, which is the case in Limnocharis, except that the nucleus stains more readily than the suspensor nucleus.

The upper daughter nucleus travels back toward the egg apparatus (*figs. 11, 12*), and by its further division forms the endosperm. At an early stage the endosperm consists of only a single layer of granular protoplasm lining the sac, in which are embedded free nuclei, as in Naias and Zannichellia; but later, in Limnocharis, walls are formed, although they are not easily distinguishable. Schaffner says that the endosperm is not abundant in Alisma; but as he does not follow the development of the embryo far, might it not be, as in the present case, that it finally completely fills the sac?

Before the polar nucleus, which forms the endosperm, has gone through the first division, fertilization has taken place; for at this time the egg nucleus has divided so that there are now two nuclei in the young embryo (*fig. 12*), and the remains of the pollen tube can be seen in many cases. Actual fusion of sperm nucleus and egg was not observed. It is evident that fertilization takes place very soon after pollination, from the fact that material killed within eighteen hours after pollination showed the embryo in a two-celled stage, with the disintegrating remains of the pollen tube near by. Fertilization probably occurs in the first night after pollination.

For the study of the development of the embryo, most of the ovules, which are U-shaped, were taken from the ovary and embedded in watch glasses for sectioning.

The first division of the egg after fertilization is transverse, and divides the cell into suspensor and embryo-cell (*fig. 13*). The original suspensor cell increases very much in size (*figs. 14–16*), has an exceptionally large nucleus, and never divides save in case of polyembryony. In this case it divides and subdivides to form an embryogenic mass, from which grow out as buds several young embryos (*figs. 17 a, b, c*), somewhat as in *Erythronium americanum* and *Tulipa Gesneri*. Whether these all mature or not I cannot say, for polyembryony is not very frequent, and I was unable to find any older stages than those shown in *figs. 17 a, b, c*, although I observed a number of younger stages.

The suspensor in the older embryo is not wholly composed of the original suspensor cell, but appropriates some of the cells that come from the first terminal segment until it contains sometimes four and even five cells (*figs. 28, 29*). The second division is always transverse (*fig. 14*), while the third division takes place in three different directions, transversely, vertically, and obliquely (*figs. 15, 18, 19*). In cases it is vertical or oblique, the growing point and the cotyledon both arise from terminal segments, agreeing with Zannichellia in this particular, but differing from Naias. After having examined a very large amount of material, I have come to the conclusion that there is no regular order of division in the active nuclei of the young embryo, at least after the first two walls are formed (*figs. 15–27*), and have thought that where descriptions do not agree it should perhaps be ascribed to the variation of development rather than to any incorrect statements or observations of the earlier writers. In *figs. 24* and *25* there are four transverse walls formed; in *fig. 25* there is no sign of division of the terminal cell; while in *fig. 24* the terminal cell is in process of division. In *fig. 16* there are three transverse walls, the terminal cell being divided vertically, while the cell next to the suspensor is in process of division.

In the further development it was impossible to follow the order of the divisions, and in the older stages of the embryo it seemed that the growing point was of lateral origin always (*figs. 22, 28, 29, 30*). The mature embryo is U-shaped (*fig. 31*), and the growing point is in the basal quarter of the embryo, apparently wholly surrounded by the epidermal layer.

This work was done at the Ames Botanical Laboratory, North Easton, Mass., under the direction of Oakes Ames.

NORTH CAMBRIDGE, MASS.

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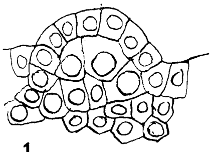

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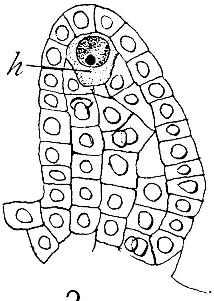

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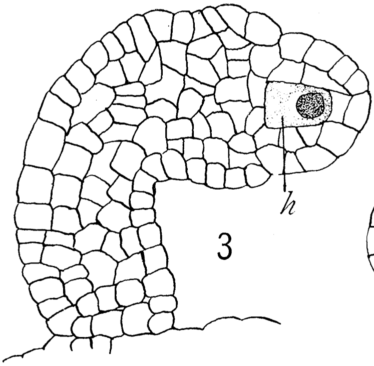

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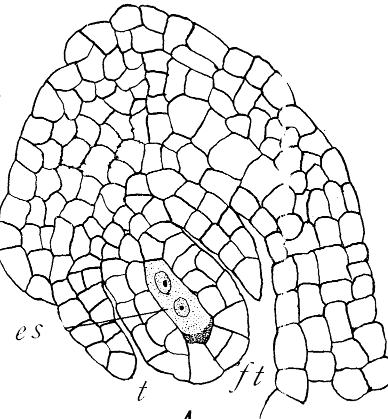

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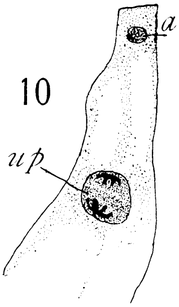

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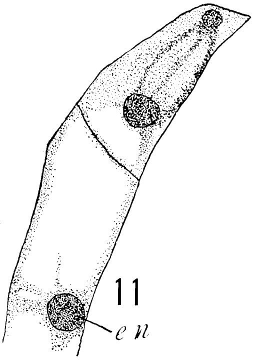

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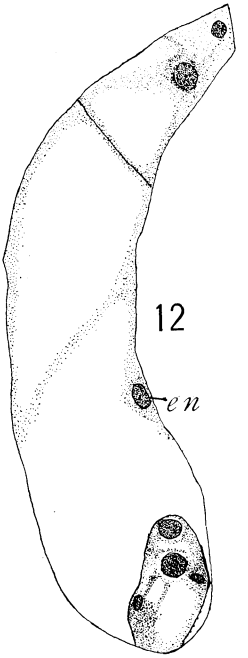

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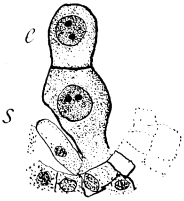

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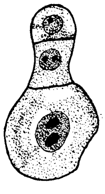

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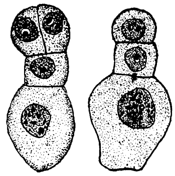

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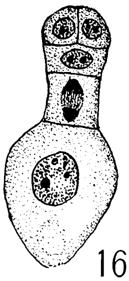

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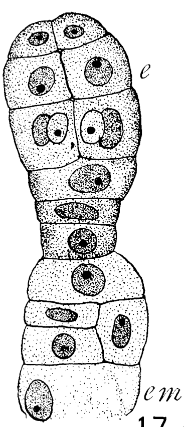

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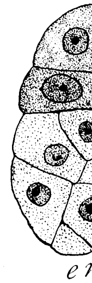

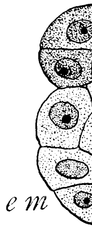

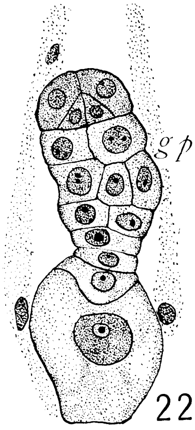

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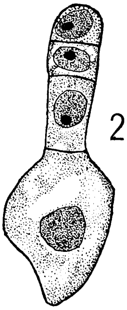

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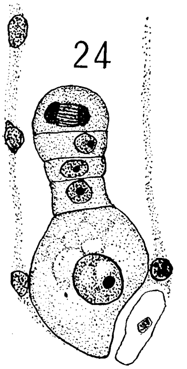

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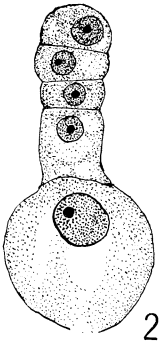

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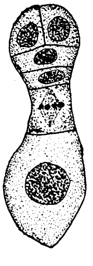

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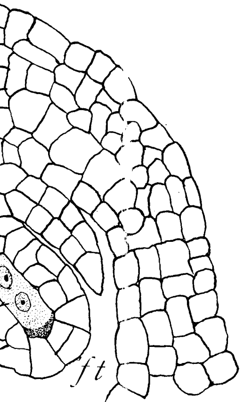
HALL on LIMNOCHA

PLATE IX



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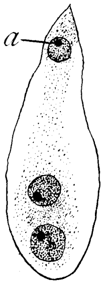

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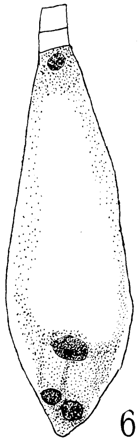

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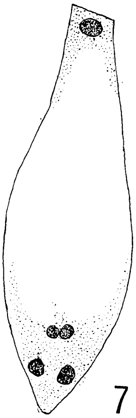

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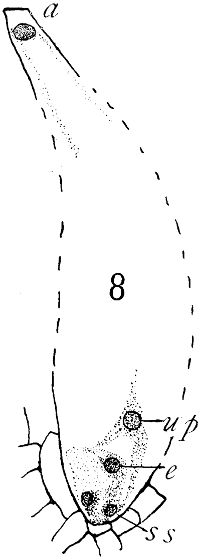

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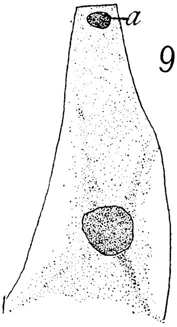

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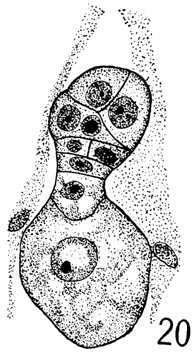

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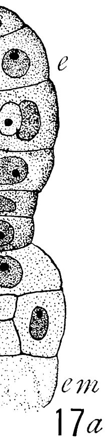

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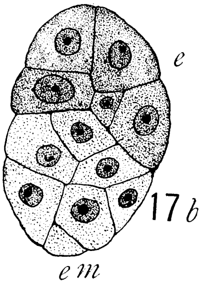

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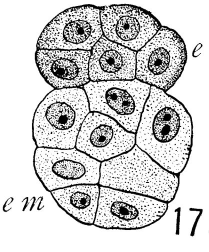

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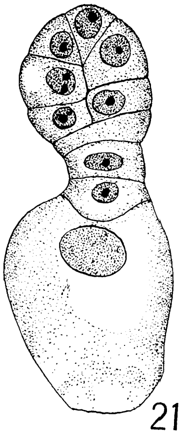

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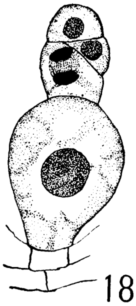

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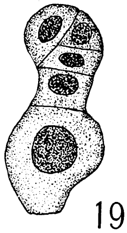

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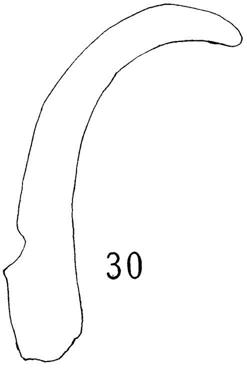

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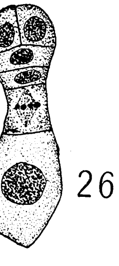

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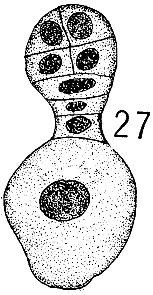

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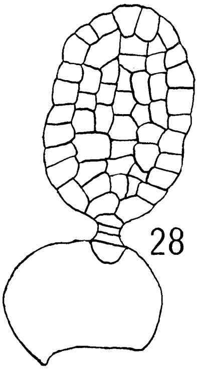

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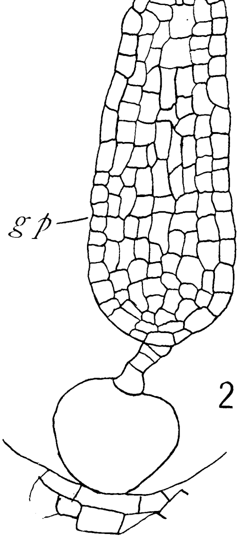

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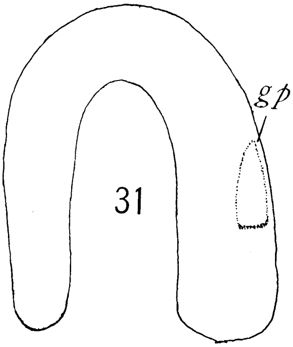

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ALL on LIMNOCHARIS

EXPLANATION OF PLATE IX.

FIG. 1 Very young ovule.

FIGS. 2, 3. Older stages of ovule showing archesporium (*h*).

FIG. 4. Ovule; *es*, embryo-sac; *ft*, false tapetal cell; *t*, tapetum.

FIGS. 5–7. Different stages of embryo-sac; *a*, antipodal.

FIG. 8. Mature embryo-sac; *a*, antipodal; *up*, upper polar; *e*, egg cell; *ss*, synergids.

FIGS. 9, 10. Lower end of embryo-sac showing antipodal (*a*) and upper polar (*up*) in process of division.

FIGS. 11, 12. Embryo-sac showing peculiar cell cut off from sac at antipodal end, and endosperm nucleus (*en*).

FIG. 13. Young embryo; *e*, "embryo-cell;" *s*, suspensor.

FIGS. 14–16. Succeeding stages of young embryo; *fig. 15*, two sections of same embryo.

FIGS. 17 *a*, *b*, *c*. Three sections of one embryogenic mass (*em*) with embryo-buds (*e*).

FIGS. 18–30. Stages of embryo; *gp*, growing point in *figs. 22–29*.

FIG. 31. Mature embryo; *gp*, growing point.